Exhibit 1

Research Article

Habitat Selection by Recolonizing Wolves in the Northern Rocky Mountains of the United States

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Abstract

*Gray wolf (*Canis lupus*) populations have persisted and expanded in northwest Montana since 1986, while reintroduction efforts in Idaho and Yellowstone have further bolstered the regional population. However, rigorous analysis of either the availability of wolf habitat in the entire region, or the specific habitat requirements of local wolves, has yet to be conducted. We examined wolf-habitat relationships in the northern Rocky Mountains of the U.S. by relating landscape/habitat features found within wolf pack home ranges (*$n = 56$*) to those found in adjacent non-occupied areas (*$n = 56$*). Logistic regression revealed that increased forest cover, lower human population density, higher elk density, and lower sheep density were the primary factors related to wolf occupation. Similar factors promoted wolf pack persistence. Further, our analysis indicated that relatively large tracts of suitable habitat remain unoccupied in the Rocky Mountains, suggesting that wolf populations likely will continue to increase in the region. Analysis of the habitat linkage between the 3 main wolf recovery areas indicates that populations in central Idaho and northwest Montana have higher connectivity than either of the 2 recovery areas to the Greater Yellowstone recovery area. Thus, for the northern Rocky Mountains to function as a metapopulation for wolves, it will be necessary that dispersal corridors to the Yellowstone ecosystem be established and conserved.* (JOURNAL OF WILDLIFE MANAGEMENT 70(2):554–563; 2006)

Key words

Canis lupus, *corridors, dispersal, habitat selection, Northern Rocky Mountains, recovery, wolves.*

By the late 1930s, gray wolf populations in the northwestern United States and southwestern Canada had been largely extirpated through human persecution (Young and Goldman 1944, Mech 1970). Following protection under the Endangered Species Act (ESA 1973), wolves began to naturally recolonize portions of the United States, including the northern Rocky Mountains (Ream and Matson 1982). The first successful production of pups by free-ranging wolves was documented in northwestern Montana in 1986 (Ream et al. 1989), and soon thereafter a small population was established in the area (Ream et al. 1991).

Lethal control of wolves that killed livestock, as well as dispersal of animals to Canada, quelled the growth rate of the establishing population in Montana (Bangs et al. 1998). However, 66 wolves were released to Yellowstone National Park and central Idaho during 1995–96, and populations in those areas have increased rapidly (Fritts et al. 1997, Bangs et al. 1998, Fritts et al. 2001). The recovery objective, establishing a minimum of 30 breeding pairs of wolves evenly distributed among the 3 recovery areas (central Id., the Greater Yellowstone Area, and northwestern Mont.; U.S. Fish and Wildlife Service 1987, U.S. Fish and Wildlife Service 1994*a*, Bangs et al. 1998) for 3 successive years, was reached in 2002 (U.S. Fish & Wildlife Service 2003). Accordingly, procedures designed to remove wolves from protection afforded by the Endangered Species Act may be initiated as soon as 2005. Despite this approaching deadline and the possibility that wolf populations in the western United States soon will be subject to changes in protection status, little effort has been made to determine the amount of available wolf habitat, potential wolf population limits, or the availability of wolf dispersal corridors in the northern Rocky Mountains of the United States.

Previous investigations of wolf habitat selection in the northern Rocky Mountains could lead to a liberal assessment of wolf habitat availability because of the inclusion of location data obtained during exploratory wolf movements (e.g., Brehme 1997, Kelley 2000). Other efforts have described wolf home ranges in the western United States through georeferencing (a process that uses known locations [e.g., cities] in a paper map to reference the location of wolf home ranges in that map) based on either published (Kelley 2000) or gray literature (Houts 2000). Yet, this approach has limited resolution for assessing wolf habitat requirements due to potential spatial biases (e.g., the type of home range analysis performed, the number of locations used to generate the home range, or clear understanding of the purpose of

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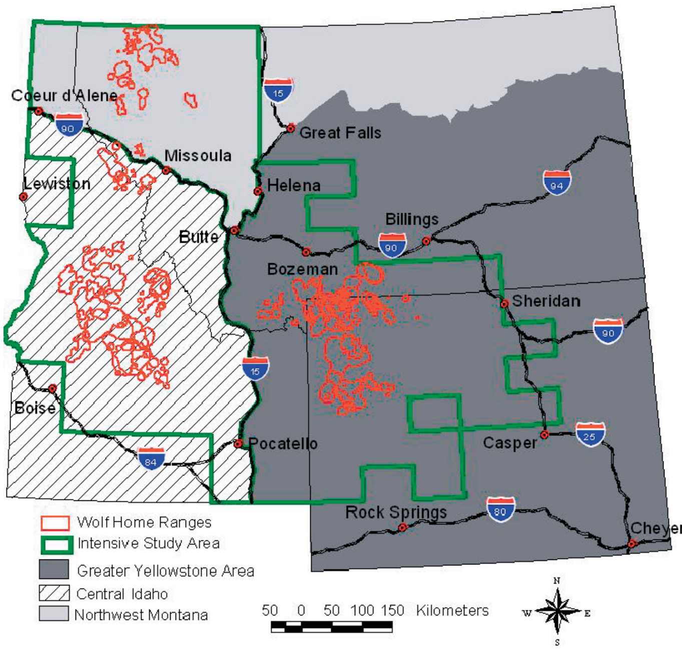

Figure 1. Study area for the wolf habitat selection in the northern Rocky Mountains, USA.

the maps as they appear in the gray literature). Recently, Carroll et al. (2003) developed a habitat selection model based on points that were generated internally and externally of wolf home ranges from Yellowstone National Park. This method, although necessary in the absence of extensive data, should be more appropriate for a fine scale analysis rather than a landscape based analysis of habitat selection (Johnson 1980). Although other authors have qualitatively described wolf habitat and dispersal requirements (e.g., Fritts et al. 1994, Fritts and Carbyn 1995), or the dispersal requirements of the northern Rocky Mountain wolf population for maintenance of genetic diversity (Forbes and Boyd 1997), a quantitative effort evaluating large-scale habitat selection patterns, habitat availability, and connectivity between recovery areas has been lacking. Such an effort would clearly be elucidating for future management plans.

In general, wolf densities are positively correlated to prey densities (Keith 1983, Fuller 1989, Fuller et al. 1992), indicating that wolves likely select areas with high ungulate density and thus should have higher rates of population growth within such areas. Further investigation of wolf habitat requirements have determined that high densities of both roads and humans were possible impediments to wolf survival, with sustainability thresholds approaching <0.70 km roads/km^2 and <4 humans/km^2 in portions of the Great Lakes region (Thiel 1985, Jensen et al. 1986, Mech et al. 1988, Fuller et al. 1992). These thresholds were found to be even lower in an expanding wolf population in Wisconsin (Mladenoff et al. 1995), indicating that selection for higher quality habitat may occur in an expanding population.

While wolves are known to disperse long distances (Fritts 1983, Ballard et al. 1987, Boyd and Pletscher 1999), currently there appears to be limited interchange of individuals between the 3 Northern Rockies recovery areas (Boyd and Pletscher 1999, U.S. Fish & Wildlife Service et al. 2000). Elsewhere (Harrison and Chapin 1998, Wydeven et al. 1998), potential wolf dispersal corridors have been evaluated using landscape-level analyses, and this approach also should be suitable for understanding connectivity between wolf recovery areas in the northern Rocky Mountains.

The objectives of the present study were to 1) determine the current patterns of habitat selection of wolves within the northern Rockies and predict future colonization probabilities within the area, 2) identify potential dispersal corridors of wolves between the 3 recovery areas, and 3) determine the landscape-scale factors that may affect wolf pack extinction probability. In general, we predicted that wolf habitat selection and pack persistence would be favored in areas where natural prey was abundant and anthropogenic influences were minimal. Yet, because of the large number of independent and potentially interacting variables under consideration, we refrain from providing specific predictions regarding habitat attributes that should be favorable to wolves and therefore suggest that our analysis should be considered as exploratory.

Study Area

The 3 wolf recovery areas identified by the U.S. Fish and Wildlife Service for the northern Rocky Mountain region are northwestern Montana (NMT), central Idaho (CID), and the Greater Yellowstone Area ([GYA] U.S. Fish & Wildlife Service 1987, 1994*a*; Bangs et al. 1998). Each of the recovery areas covers $>$ 50,000 km^2, with a mixture of primarily public and some private lands (Fig. 1). Elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and moose (*Alces alces*) were the major prey species within the recovery areas (U. S. Fish & Wildlife Service 1994*b*). Domestic livestock occurred throughout the region, with the exception of the majority of National Parks and wilderness areas (U.S. Fish & Wildlife Service 1994*b*). Vegetation was characterized by a variety of habitat types, ranging from sage covered foothills to forested mountains (U.S. Fish & Wildlife Service 1994*b*).

Methods

Home Ranges

We used aerial locations of wolves in each of the 3 recovery areas to develop home ranges for the habitat selection portion of this study (White and Garrott 1990). We based home range polygons on 1 year (Jan–Dec) of locations evenly distributed across summer and winter seasons for wolves from a given pack (Mladenoff et al. 1995, Wydeven et al. 1995). In order to maximize sample independence, we recognized individual locations for radiomarked wolves that were either spatially or temporally separated from other radiomarked pack members; this approach limited potential autocorrelation of locations.

Wolf home range size has been shown to reach an asymptote at around 30 locations and increasing the number of locations beyond this level has little effect (Carbyn 1983, Fuller and Snow 1988). Alternatively, some authors have suggested that in recolonizing wolf populations, a larger number of locations may be required for home range size to reach its asymptote (Fritts and Mech 1981). Recognizing that some wolf populations in the northern Rockies occur in remote areas and thus are not monitored intensively, we elected to use $\geq$20 locations per year as a threshold of retention in our database. We used the fixed kernel method to estimate wolf home ranges due to its low bias

Table 1. Spatial data used to construct wolf habitat models and the type of data analysis performed with each theme.

Layer	Resolution	Data source	Analysis type[a]
Bailey's ecoregions		USFS[b]	A
Road density	90 m	ID[c], WY[d], MT[e]	A, B, C, E
Human density	Block groups	USBC[f]	A, B, C, D, E
Protection status	90 m	GAP[g]	A, B, C, E
Land ownership	90 m	GAP	A, B, C, E
Slope	90 m	USGS[h]	B, C, E
Elevation	90 m	USGS	B, C, E
Land cover[i]	90 m	GAP	B, C, D, E
Ungulate density	GMU	Harvest[j]	B, C, D, E
Cattle density	County	USDA	B, C, D, E
Sheep density	County	USDA	B, C, D, E
Wolf home ranges		USFWS[k]	A, B, C, D, E

[a]A = 1:100,000 quadrangle study area definition, B = Conservative logistic regression of use and non-use, C = Liberal logistic regression of use and nonuse, D = Dispersal corridor analysis, E = Pack persistence analysis.
[b]U.S. Forest Service.
[c]Idaho Department of Water Resources.
[d]Wyoming Geographic Information Science Center.
[e]Montana Natural Resource Information System.
[f]U.S. Bureau of Census.
[g]National GAP.
[h]U.S. Geological Survey.
[i]Land Cover was reclassified into 7 percent cover classifications (Forest, Shrub, Desert, Human, Grass/Agriculture, Riparian/water, and Other).
[j]Based on ungulate game harvest data collect by state Fish and Game agencies.
[k]Data collected by U.S. Fish and Wildlife Service, Yellowstone National Park, and Nez Perce Tribe. Home ranges were composed by the authors.

when sample sizes are small (Kernohan et al. 2001). In contrast, previous wolf home range analysis has relied largely on the less stable and less accurate minimum convex polygon (MCP) method (e.g., Fritts and Mech 1981, Carbyn 1983, Fuller and Snow 1988, Burch 2001). Fixed kernel home ranges derived from smaller sample sizes typically yield larger home range size estimates (Seaman et al. 1999, Powell 2000, Kernohan et al. 2001), which for habitat selection analysis should minimize the differences between wolf used and unused areas and thus create a more conservative assessment of habitat selection. For our sample (56 home ranges), 18% had 20–23 locations, 21% had 24–29 locations, and the remainder (61%) had >29 locations. We generated home range polygons at the 95% and 50% levels to represent home range and core use areas (White and Garrott 1990), using the fixed kernel method (Worton 1989) with least-squares cross-validation (LSCV) as the smoothing option in the animal movement extension in the program Arcview (Hooge et al. 1999; ESRI, Redlands, California, USA).

Initially, we described home range sizes for the packs in each of the 3 recovery areas. Within each recovery area, we randomly created an equivalent number of circular nonpack home ranges (controls) to mimic wolf home ranges in areas not currently occupied by wolves. Nonpack areas were the size of the average wolf home ranges for the 95% fixed kernel level of the respective recovery area. We overlaid both pack and nonpack areas on spatial data using Geographic Information System (GIS) to determine the spatial attributes of the entire home range and nonuse areas. Although most packs occupied similar home ranges for several years, we only used 1 wolf pack-year as the basis for the comparison. We used all wolf pack-years to exclude areas from which non-use areas could be selected. We selected the specific pack-year for analysis by maximizing radio-location sample sizes and minimizing the time span to our reference year (2000).

Spatial Data

We assessed a suite of habitat and landscape-level attributes in relation wolf home range use (Table 1). We derived slope and elevation data from digital elevation models (DEMs), while we separated road density data (km of roads/km^2) into 2 variables: 1) the density of roads passable by a 2-wheel-drive vehicle, and 2) the density of 4-wheel-drive roads.

We based ungulate density information on unpublished harvest statistics provided by the states of Idaho, Montana, and Wyoming, while livestock density was based on U.S. Department of Agriculture statistics for counties. We averaged total cattle (nondairy) and sheep numbers across a 5-year period (1995–2000) for each county, and linked with a county layer to generate livestock densities for the region. We excluded wilderness and national parks from counties to ensure that livestock density estimates encompassed only areas where grazing occurred. We divided land ownership into 4 classifications (private, federal, state, and water), and vegetation cover into 7 types based on national GAP data (forest, shrub, urban, desert, grass/agriculture, riparian/water, and other [rock and ice]). For our analysis of factors promoting pack persistence (see below), we used urban/agriculture and grass as classifications rather than grass/agriculture and urban. This allowed for vegetation cover with similar wolf mortality risk to be grouped in the persistence analysis, and vegetation cover with similar landscape features to be grouped in the habitat analysis.

We did not use population estimates for game management units (GMU) to describe ungulate densities because population estimation techniques and intensity of monitoring varied for states, GMUs, and ungulate species. Instead, we compared available aerial flight population estimates for GMUs with various recorded harvest statistics (e.g., days per harvest, percent successful harvest, etc.), to arrive at an index for ungulate density that could be applied across jurisdictions. Using stepwise linear regression, we confirmed that total harvest was the most strongly correlated index for both mule deer ($r = 0.71$, $t = 4.776$, $P < 0.001$, root mean square error (RMSE) $= 0.763$, $n = 25$) and elk ($r = 0.64$, $t = 9.309$, $P < 0.001$, RMSE $= 0.624$, $n = 126$) density estimates. Accordingly, total harvest was averaged for a 5-year period (1995–2000) across each GMU and then described as high, medium, or low based on the quartiles of distribution for all GMUs. We classified areas where hunting was not permitted or the state agency did not have information (e.g., National Parks and reservations) based on the average of the GMUs along their respective border.

Habitat Selection Analysis

Habitat analysis can be greatly influenced by the extent of the study area chosen to represent available habitat (McClean et al. 1998, Garshelis 2000, Huston 2002). We chose to examine areas used by wolf packs versus those currently unused (controls), across several spatial scales. The study population was intensively monitored (all reintroduced wolves were collared, and extensive efforts were made to capture individuals from packs lacking

collared animals to count these packs towards recovery). Accordingly, we believe that the sampling protocol represents a de facto 'use versus non-use' design (see Manly et al. 2002). Thus, we first defined our intensive study area by allowing control areas to be placed randomly within the unoccupied portion of the recovery area, and used logistic regression to compare habitat attributes for wolf packs versus unused areas (controls). This analysis provided a preliminary model of wolf habitat selection similar to a first-order selection (see Johnson 1980). We used several landscape-scale GIS layers as the basis for comparisons between use and nonuse areas (Table 1). We then placed attributes identified as important in this analysis within a 1:100000 quadrangle grid to define an intensive study area boundary for which refined analysis of wolf habitat selection patterns could occur. We identified 2 significant factors in this comparison. First, all wolf packs contained a majority of the temperate-steppe-mountain division of the Bailey's ecoregion layer (Bailey 1983). This variable was categorical, and therefore, in the regression there were 2 empty cells (e.g., no wolf packs occurred in temperate-desert or temperate-steppe ecoregions). Logistic regression creates unreliable coefficient estimates with large standard errors when empty cells are present in a categorical variable (Hosmer and Lemeshow 2000). Thus, we simply considered any 1:100000 quadrangle which contained a portion of the temperate steppe mountain regime as part of the intensive study area. Protection status, a categorical variable designed to represent how well a particular piece of land is protected (e.g., wilderness areas are highly protected with no roads or livestock use) was the only other variable identified as significant in the landscape scale logistic regression ($t = 3.965$, $P < 0.001$, change in Aikike's Information Criterion [ΔAIC] = –22.04, $n = 112$). To be conservative, we selected any remaining 1:100000 quadrangle that had a probability of wolf occurrence $\geq$0.25 according to the following formulae:

$$logit(p) = -4.575 + 1.531(protection\,status) \tag{1}$$

$$p = e^{logit(p)}/1 + e^{logit(p)} \tag{2}$$

Thus, we generated an intensive study area boundary with scientific reasoning, rather than an arbitrary definition of study area, as has been problematic in previous efforts (McClean et al. 1998, Garshelis 2000). Thereafter, we conducted a more refined habitat analysis (e.g., a Johnson [1980] second-order selection), in which nonuse areas were restricted to our above defined intensive study area in unoccupied areas. We analyzed logistic regression comparisons between use and nonuse areas, with ΔAIC_c values > 2.0 used to determine candidate models that had a better fit (Anderson et al. 2000). We used independent variables that were 1) significant in univariate analysis, 2) not-correlated to other variables ($r \leq 0.70$, see Hosmer and Lemeshow 2000) within the data set, and 3) represented $\geq$5 percent of the landscape, as candidate variables. We defined 2 nonuse levels for comparison to wolf home ranges: 1) a conservative model (considered conservative because it should minimize the differences between use and nonuse) in which nonuse areas were only exclusive of pack areas for the year in which wolf home ranges were being considered as "used" (this resulted in 9% of the control area within portions of once occupied wolf territory), and 2) a liberal model, in which nonuse areas were exclusive of all wolf-year home ranges. This design enabled comparisons between the conservative and liberal models to assess the effect of slight violations to a strict use versus non-use study design (Manly et al. 2002). Although it is unlikely that the liberal model would include unused areas occurring within unknown occupied wolf territories, it is possible that a small number of dispersal locations or future colonization areas could be included, thereby warranting comparisons to the conservative model.

We checked continuous variables that were retained in the model for linearity via the quartile method (Hosmer and Lemeshow 2000). Further, we checked variables that showed slight deviations from linearity for possible biologically relevant transformations (e.g., categorical, cut points, and quadratic) that could improve the model (Hosmer and Lemeshow 2000). Finally, we tested all 2-way and 3-way interactions between significant variables for possible inclusion. We tested final models with the Hosmer and Lemeshow goodness-of-fit test statistics (HL Stat) to ensure model fit and appropriate data transformations (Hosmer and Lemeshow 2000). We calculated probabilities of wolf colonization for each wolf home range and nonuse area. We described sensitivity (proportion of used areas predicted to be used), specificity (proportion of nonuse areas predicted to be nonuse), false positive rate (proportion of predicted use areas that were nonuse), and false negative rate (proportion of predicted nonuse areas that were used), for the final regression models (Hosmer and Lemeshow 2000, Manen et al. 2000). We defined the cut point between use and nonuse at the 0.5 colonization probability level. Thus, we referred to habitat $\geq$0.5 colonization probability as high quality wolf habitat likely to be occupied by wolves currently or in the future. To further evaluate model robustness, we tested each model against 8 wolf home ranges that were excluded from model development because of a small number of locations (mean no. locations: 13.9 +/- 1.0 [SE]). We generated probabilities across the landscape in 1:24000 quadrangle cells for wolf occupancy, and in 9-km^2 cells for dispersal corridor analysis. Wolves generally can disperse across habitat that is poorer than that required for colonization (Harrison and Chapin 1998, Mech and Boitani 2003). Thus, we arbitrarily identified dispersal corridors by wolf presence probabilities $\geq$0.30 in the 9-km^2 cell grid. By relaxing our colonization standards, we conformed to the practice of favoring less stringent standards to determine dispersal habitat (see Harrison and Chapin 1998).

We conducted additional statistical tests including 1) a Kruskal-Wallis tests (Sokal and Rolf 1981) for comparing between wolf use and non-use control areas, 2) a 1-sample t-test comparing between pack habitat characteristics versus those found in the intensive study area, and 3) a paired t-test between 95% fixed kernel home ranges and 50% fixed kernel core use areas examining landscape/habitat features that differed between core versus noncore portions of wolf home ranges. We considered comparisons between core use areas and home ranges to represent a conservative assessment of potential differences between the 2 scales of analysis, because 50% cores were found within a portion of the 95% home range, thus reducing the potential differences between samples.

Table 2. Mean (± SE) landscape variable characteristics for wolf pack territories (95% fixed kernel) and core use areas (50% fixed kernel [$n = 56$]), conservative and liberal definitions for nonuse areas ($n = 56$), in the northern Rocky Mountain study region, USA.

Variable	Pack territories	Pack core use	Nonuse conservative	Nonuse liberal	Study area
Land cover (%)					
Urban	0.07(0.02)	0.06(0.03)	0.23(0.09)	0.31(0.11)	0.26[b]
Grass/agriculture	11.76(1.48)	11.72(2.17)	17.41(1.65)[a]	23.51(2.51)[a]	23.14[b]
Shrubs	13.71(1.54)	13.13(1.82)	24.24(3.04)	30.70(3.45)[a]	23.78[b]
Desert	0.10(0.06)	0.00(0.00)	7.22(2.58)[a]	2.32(1.07)[a]	2.49[b]
Forest	68.21(2.06)	67.42(2.57)	42.36(3.83)[a]	34.59(3.69)[a]	43.08[b]
Other (rock/ice)	2.38(0.49)	2.04(0.53)	5.37(1.25)[a]	4.57(0.79)	3.55[b]
Riparian/water	3.78(0.45)	5.23(1.18)	3.17(0.36)	4.00(0.81)	3.70
Land ownership (%)					
Federal	83.67(3.24)	81.59(3.81)	73.30(2.84)[a]	65.04(3.48)[a]	65.27[b]
Private	13.60(2.96)	15.89(3.50)	22.27(2.54)[a]	27.91(3.08)[a]	28.94[b]
State	1.98(0.57)	1.57(0.63)	3.89(0.72)[a]	5.74(1.15)[a]	4.79[b]
Density[c]					
2-Wheel-drive roads	0.44(0.06)	0.44(0.07)	0.62(0.05)[a]	0.64(0.05)[a]	6.48[b]
4-Wheel-drive roads	0.10(0.02)	0.12(0.03)	0.06(0.01)[a]	0.08(0.02)	0.09
Human	0.43(0.07)	0.33(0.06)	2.26(0.98)[a]	2.41(0.78)[a]	2.44[b]
Sheep	0.24(0.04)	0.25(0.06)	1.06(0.18)[a]	1.09(0.15)[a]	1.01[b]
Cattle	2.50(0.34)	2.63(0.41)	6.02(0.48)[a]	6.61(0.53)[a]	5.71[b]
Coded variables[d]					
Mule deer	1.64(0.07)	1.66(0.08)	1.84(0.08)	1.88(0.08)[a]	1.86[b]
White-tailed deer	1.60(0.10)	1.61(0.10)	1.69(0.11)	1.52(0.10)	1.67
Elk	2.20(0.09)	2.22(0.09)	1.70(0.11)[a]	1.68(0.11)[a]	1.84[b]
Protection status	2.46(0.11)	2.50(0.12)	2.98(0.08)[a]	2.99(0.09)[a]	3.04[b]
Topography					
Slope	11.64(0.42)	10.34(0.58)[e]	9.88(0.74)	8.66(0.68)[a]	9.22[b]
Elevation	2025.7(60.9)	1981.9(66.2)[e]	1848.0(70.6)[a]	1820.2(60.3)[a]	1799.7[b]

[a]Kruskal-Wallis test compared with pack territories was significant for the variable at $P < 0.05$.
[b]Single sample t-test compared with pack territories was significant for the variable at $P < 0.05$.
[c]Density measured as km/km^2 for road variables and no./km^2 for human, cattle, and sheep.
[d]Coded variables were weighted averages for the area and went from low (1) to high (3) for elk, mule deer, and white-tailed deer. Protection status was coded with four categories with high protection receiving a value of 4.
[e]Paired t-test significant ($P < 0.05$) in comparisons between the variable and pack territories.

Habitat Associations and Population Dynamics

We examined wolf demographic patterns (i.e., pack persistence) relative to our predicted probability values within the liberal habitat selection model, as well as in comparison to a variety of landscape/habitat characteristics of relevance. We built pack persistence models using logistic regression with the dependent variable based on the pack's extinction status (0 = Extinct, 1 = Survived; see methods described previously for the habitat selection analysis).

Results

Habitat Selection

We established polygons for each of the 64 wolf packs included as occupied wolf territory in the analysis, which totaled 198 pack years. However, only 56 packs in 154 pack years had an adequate number of locations ($\geq$20) to use for data analysis. The average ($\pm$SE) number of annual locations per home range was 36 $\pm$ 1.7 ($n = 58$), 33 $\pm$ 2.8 ($n = 27$), and 60 $\pm$ 2.5 ($n = 69$) for CID, NMT, and the GYA areas, respectively. Core use areas differed significantly from home ranges for slope and elevation variables, with core use areas being characterized by lower elevation and slope (Table 2).

Univariate analysis identified several landscape characteristics that were significantly related to the presence of wolves within the intensive study area (Table 2), suggesting that a large number of possible models could potentially describe areas in which wolves are likely to occur. Six variables were spatially correlated ($r > 0.70$ [federal ownership and private ownership -0.959; human density and urban land cover 0.867; forest land cover and shrub land cover -0.762]) within the data set. We retained federal ownership, human density, and forest land cover for analysis. Several candidate models explained the patterns of wolf habitat selection in the liberal model (Table 3). Our best liberal model showed a positive relationship between wolf presence and both forest cover and elk density variables, and a negative relationship with human and sheep densities. Variables in the best liberal model conformed to the assumption of linearity, and performed well in model fit tests ($R^2 = 0.491$, HL stat $= 8.444$, $P = 0.295$, $df = 7$). The best conservative model showed a positive relationship between wolf presence and both forest cover and elk density, and a negative correlation with human and cattle densities. Thus, the conservative model was generally similar to the liberal model, and the close association among variable characteristics from both model types (Table 2) was indicative of overall model robustness.

We placed the results for each model in formula 2 (see Methods section) to generate probabilities for all used and nonused areas, to further examine model performance. The conservative and liberal models both performed well with regards to sensitivity (44 of 56 [0.79], and 49 of 56 [0.88] wolf use areas predicted correctly, respectively) and specificity (44 of 56 [0.79] and 46 of 56 [0.82]

Table 3. Models supported within the liberal logistic regression analysis for wolf habitat selection in the northern Rocky Mountain wolf population. Models were based on 56 wolf home ranges compared with 56 nonuse areas.

Model[a]	AIC_c	ΔAIC	w_i
−4.457 + (0.057) Forest cover + (−0.87) human dens. + (1.351) Elk + (−1.735) sheep dens.	89.56	0.00	0.589
Forest cover + human dens. + elk + cattle dens.	91.15	1.59	0.267
Forest cover + human dens. + elk	92.96	3.40	0.108
Forest cover + cattle dens. + elk	97.40	7.84	0.012
Forest cover + sheep dens. + human dens.	97.47	7.91	0.011
Forest cover + sheep dens. + elk	98.80	9.24	0.006
Forest cover + cattle dens. + human dens.	99.71	10.15	0.004
Forest cover + human dens.	99.98	10.42	0.003
Forest cover + elk	102.54	12.98	0.001

[a] Coefficient estimates were only included for the top model. A constant term was included in all models and used for calculation of AIC.

nonuse areas predicted correctly, respectively). In contrast, false positive and false negative rates were relatively low (0.12–0.21) for the models. Each of the models predicted site occupancy for 7 out of 8 wolf packs that were not used to develop the models.

To assess the amount of habitat available in the 3 recovery areas, we generated probabilities for the liberal model in 1:24000 quadrangle grids (Fig. 2) and 9 km^2 grids (Fig. 3). We found that the CID recovery area had the greatest amount of high quality wolf habitat (colonization probability $\geq$0.5; 77,596 km^2), while the GYA (45,900 km^2) and the NMT (44,929 km^2) recovery areas had similar amounts of high quality wolf habitat (Table 4).

When wolves are removed from protection of the Endangered Species Act (ESA), wolf management will be conducted at the state level rather than at the recovery area level. Our model predicted that at that time, the jurisdictional breakdown of high quality wolf habitat would change to 72,012, 69,490, and 28,725 km^2 for Idaho, Montana, and Wyoming, respectively (Table 4).

Dispersal Corridors

Our assessment of dispersal corridors detected solid linkages between the NMT and CID recovery areas, with large potential corridors comprised of suitable habitat connecting the core areas in both regions (Fig. 3). Further, there appears to be appropriate dispersal habitat in western Idaho to allow for wolf dispersal

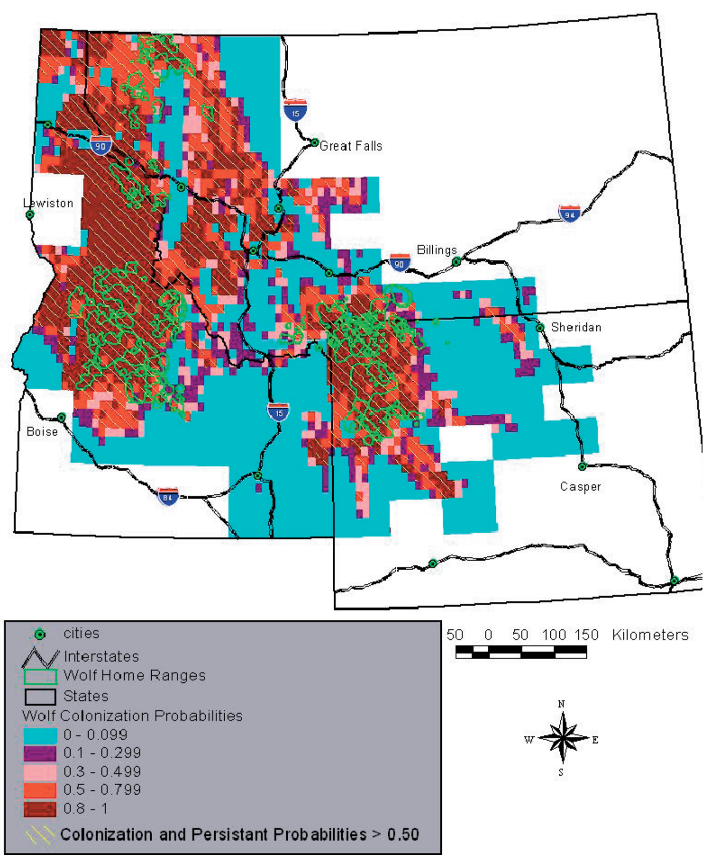

Figure 2. The probability of wolf occupancy and wolf pack persistence predicted for the northern Rocky Mountains, USA. Maps were derived using 1:24,000 quadrangles.

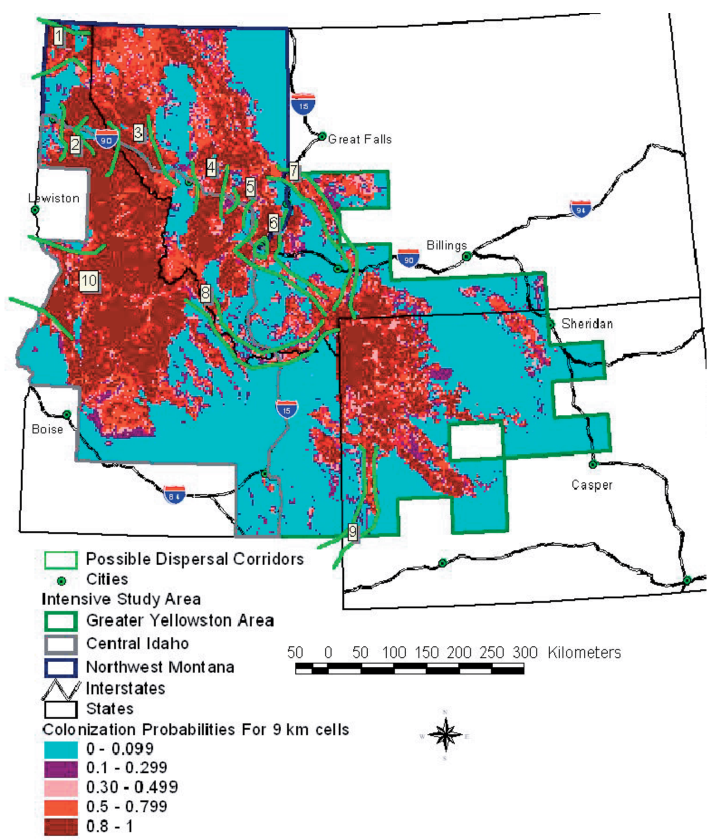

Figure 3. Ten possible wolf dispersal corridors defined in the northern Rocky Mountains, USA.

Table 4. Area (km^2) of wolf colonization probabilities based on a logistic regression modelwithin the intensive study region (see Fig. 1) for current recovery areas (northwest Mont. [NMT], Greater Yellowstone Area [GYA], and Central Id. [CID]) and individual states (Mont., Wyo., and Id.).

	Area of colonization (km^2)					
Probability	NMT	GYA	CID	Montana	Wyoming	Idaho
>0.90	14,382	22,144	47,219	23,086	16,604	44,992
44,992 0.75–0.90	18,330	11,023	17,394	25,875	5,647	15,672
0.50–0.74	12,217	12,734	12,983	20,529	6,473	11,347
0.25–0.49	7,182	14,748	8,938	15,557	7,139	8,356
0.10–0.24	5,097	14,703	8,688	13,772	6,322	8,302
0.00–0.09	25,895	111,351	55,248	58,480	59,723	72,403

outside of the recovery region into Oregon and Washington. However, the GYA recovery area appears to be poorly linked to the other populations through relatively narrow and largely discontinuous corridors of appropriate habitat (Fig. 3).

Habitat Associations and Population Dynamics

Pack persistence analysis for the 56 (43 extant, 13 extinct) wolf packs revealed a relatively simple best model in which private ownership and agriculture/urban vegetation were the only 2 variables included. In this analysis we used private ownership rather than federal ownership (these 2 variables were collinear $r = -0.959$), because ancillary analysis indicated that federal ownership was related to pack persistence in a nonlinear fashion. Additional analysis of private ownership indicated that a nonlinear relationship failed to provide superior explanatory power. The model that best described pack persistence was

$$logit(p) = 2.364 + (-0.041 * PercentPrivateOwnership) + (-0.708 * PercentAgriculture/UrbanVegetation) \quad (3)$$

This model provided satisfactory diagnostics (HL stat $= 7.3$, $P = 0.505$, $df = 8$), and correctly predicted 6 out of 8 packs excluded from model development due to small sample sizes. Although not retained in our final persistence model, the variable representing wolf colonization probabilities was included in the fourth best model (Table 5). Next, we multiplied the probability for pack persistence by the probability of wolf colonization to examine the areas where wolves are likely to colonize and persist in the future (Fig. 2). This procedure revealed that extinction probabilities could potentially limit wolf packs near the edges of each of the 3 recovery areas (Fig. 2). However, only a 1% decline in total high quality wolf habitat was observed by selecting areas with a ≥ 0.5 probability of persistence and colonization of areas (Fig. 2). Thus, we consider that only nominal wolf population limitation is likely to occur due to losses at the edge of the region of suitable habitat.

Discussion

Wolf Habitat Selection and Population Consequences

Our model detected positive correlations with environmental factors (forest cover and elk) and negative correlations between wolf occupancy and anthropogenic factors (human density and domestic sheep density). Each significant variable appears to be intuitively relevant to wolf survival and pack persistence, except perhaps domestic sheep density. Yet, it seems likely that retention of this latter parameter is related to lethal control of individual wolves following depredation events, and thus preventing pack formation in these areas. Similarly, human density likely functions as an indication of high wolf mortality in areas of increased human presence. Elk are considered the primary prey for wolves within the region (Bangs et al. 1998), thus, selection of areas with increased elk densities is of particular biological relevance for wolf survival, production, and habitat use.

In general, wolves potentially could live in any area where human tolerance and prey populations are adequate to support viable numbers (Mech 1970, Keith 1983, Fuller 1989, Mech 1995, Fritts et al. 2003). For instance, the presence of wolves in the northeastern United States has been principally described by landscape scale attributes (density of 2-wheel-drive roads) related to human mortality risk (Mladenoff et al. 1995, Harrison and Chapin 1998, Mladenoff and Sickley 1998, Wydeven et al. 1998). This relationship is based on the apparently low wolf survival and colonization rates in areas of high road density (Theil 1985, Mech et al. 1988, Fuller et al. 1992, Mladenoff and Sickley 1998, Wydeven et al. 2001). The widely-accepted model by Mladenoff et al. (1995) has been effective in predicting future colonization of wolves in Michigan and Wisconsin (Mladenoff and Sickley 1998,

Table 5. Models supported within the pack persistence regression analysis for the northern Rocky Mountain wolf population. Models were based on 43 extant wolf home ranges compared with 13 extinct wolf home ranges.

Model[a]	AIC_c	ΔAIC	w_i
Private ownership + agriculture/urban cover	55.45	0.00	0.572
Private ownership	57.45	2.00	0.210
2-Wheel drive road density	59.33	3.88	0.082
Liberal model probabilities	59.50	4.05	0.075
Protection status	60.77	5.32	0.040
Elk	62.09	6.65	0.021

[a] Coefficient estimates were included in the text for the top model. A constant term was included in all models and used for calculation of AIC.

Mladenoff et al. 1999) based on landscape scale attributes (2-wheel-drive roads) related to human mortality risk. Yet, this model was originally based on a small sample of packs ($n = 14$) relative to that commonly required for development of robust logistic regression models (see Hosmer and Lemeshow 2000). Also, the model developed by Mladenoff et al. (1995) may not be best suited for predicting wolf occupancy in areas where populations may be limited by different factors than those occurring in the Great Lakes region. Therefore, our analysis should be more appropriate for examining wolf-habitat relationships in the western United States because it is based on a larger sample of observations and relates site-specific habitat attributes to wolf colonization and persistence within the local landscape (Oakleaf 2002). The recent model by Carroll et al. (2003) was restricted to the GYA recovery area only and is substantially less parsimonious than our model (10 vs. 4 parameters). Therefore, our analysis should provide relevant insight as to the factors promoting wolf habitat occupancy and pack persistence in the northern Rockies.

Other models designed to predict wolf density as a function of prey density (e.g., Keith 1983, Fuller 1989), must be used guardedly under the present circumstances because they emphasize wolf populations that are subject to density-dependent constraints rather than those that are expanding to new habitat. Because it appears that wolves are unlikely to fully saturate potential areas of colonization in the western United States due to the patchy distribution of high quality habitat and the heterogeneous distribution of their primary prey (elk) in the region, wolf density predictions based exclusively on prey density or biomass estimates are likely to be too liberal.

Dispersal

Wolves are able to travel through relatively poor habitat in order to colonize new areas (Mech et al. 1995, Merrill and Mech 2000). However, such dispersal corridors are less than desirable because they expose dispersers to higher mortality risk and thus can result in poor connectivity between populations. Our dispersal habitat model was based on colonization probabilities, with a relatively low colonization threshold (>0.3) used to characterize corridors. Our analysis revealed that wolf populations in NMT and CID recovery areas appear to be linked by contiguous tracts of quality habitat; several wolves (8, with 3 contributing offspring) already are known to have successfully dispersed between these recovery areas (J. Fontaine, U.S. Fish and Wildlife Service, Helena, Mont., USA, unpublished data). In contrast, the linkage between the GYA and other recovery areas is more suspect, and this pattern is consistent even when the threshold for dispersal habitat is reduced substantially (>0.1 probability of colonization, see Fig. 3). This finding is supported by limited documented dispersal between the GYA and the remaining recovery areas. In fact, 5 of the 6 documented dispersals between the GYA and other recovery areas resulted in either death, disappearance or relocation of the disperser (D. Smith, Yellowstone Center for Resources, Yellowstone National Park, Wyo., USA, unpublished data). However, recently a successful dispersal has been documented from Idaho to the GYA, showing that dispersals to or from the GYA remain possible. However, for the northern Rocky Mountain wolf population to effectively function as a metapopulation, it will be desirable to prioritize the protection and perhaps restoration of dispersal linkages between the GYA and other recovery areas. This objective may be problematic because much of the candidate lands are privately owned.

Habitat Associations and Population Dynamics

Pack extinction rates appeared to be correlated with colonization probabilities for wolves, suggesting that our colonization model accounted for areas where wolves were likely to remain extant through time. Interestingly, only 2 parameters were retained within the best pack persistence model (private ownership, and agriculture/human vegetation cover), implying that livestock depredations and subsequent control actions probably are more prevalent on private land (see Bangs et al. 1998, Mack et al. 2002). In the future, survival analysis for individual radiocollared wolves should further elucidate the relationship between various anthropogenic factors and wolf mortality risk.

Management Implications

Our results suggest that wolf numbers are likely to continue increasing in the northern Rocky Mountains due to the availability of high-quality habitat (e.g. colonization probabilities ≥ 0.5) and adequate dispersal corridors between certain subpopulations. Further, potential corridors exist that could facilitate wolf dispersal into adjacent states (Ut., Oreg., and Wash.). Indeed, to date at least 1 wolf from the recovery areas is known to have dispersed to each of these states (Joe Fontaine, U.S. Fish and Wildlife Service, Helena, Mont., USA, unpublished data). State management agencies in these areas should be prepared and expect continued dispersal and eventual colonization of wolves. However, to better predict potential wolf habitat occupancy, dispersal, and potential for population growth in the entire western United States, it remains necessary to pursue additional habitat assessment in currently unoccupied states.

State agencies currently planning to assume wolf management responsibilities over extant populations should consider how new jurisdictional boundaries will affect the amount of estimated preferred habitat within each of the states. Under state management, Wyoming should consistently have the fewest number of packs within the system because of the small amount of preferred habitat relative to that in Idaho and Montana. This will pose challenges to state agencies in terms of balancing wolf population viability and post-delisting monitoring requirements between jurisdictional boundaries while maintaining public support for wolf management within the individual state.

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